Trade-Offs in Body Weights, Egg Loads, and Fat Reserves of Field-Collected *Podisus maculiventris* (Heteroptera: Pentatomidae)

JESUSA CRISOSTOMO LEGASPI,[1] ROBERT J. O'NEIL,[2] AND BENJAMIN C. LEGASPI, JR.

Biological Control of Pests Research Unit, USDA, ARS–Subtropical Agricultural Research Laboratory,
2413 East Highway 83, Weslaco, TX 78596

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ABSTRACT The spined soldier bug, *Podisus maculiventris* (Say), was collected in 8 field sites in Indiana during the summers of 1987–1989. The insects were collected using both pheromone traps and sweep nets. Insect weights were recorded for all 3 yrs, and egg loads and lipid content in the fat body were recorded for 1988 and 1989. Analysis of the weights revealed that females were heavier than males. Female body weight, egg load, and lipid content were compared against corresponding measurements of predators subjected to different prey regimens in the laboratory. These comparisons indicate that field populations often had measurements similar to predators provided 1 prey item every 3–9 d. Predators collected during the summer of 1988 revealed higher mean lipid content, smaller egg loads, and lower weights than those collected in 1989. These traits, together with the relative scarcity of predators found in 1988, suggest that the predators were responding to greater food stress by conserving energy reserves in the fat body and diverting them away from reproduction. We discuss possible implications of these observations.

KEY WORDS *Podisus maculiventris*, lipids, fat reserves, trade-off

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ESTABLISHMENT OF predator populations in any environment requires that they be capable of finding sufficient numbers of prey to survive and reproduce. In cases where prey resources are scarce, the maintenance of the predator population depends on their ability to allocate scarce energy resources among competing physiologic demands. For example, the predatory mite *Zetzellia mali* (Ewing) reduces oviposition and feeding rates in food-scarce environments (Santos 1982). Chua and Mikil (1989) found the same response in the mirid predator *Cyrtorhinus lividipennis* Reuter feeding on the rice brown planthopper *Nilaparvata lugens* (Stål). The spined soldier bug, *Podisus maculiventris* (Say), reduces reproductive effort while maintaining longevity and body weight when provided low numbers of yellow mealworm larvae, *Tenebrio molitor* L., as prey (O'Neil and Wiedenmann 1990, Wiedenmann and O'Neil 1990). De Clercq and Degheele (1992) found the same response in *Podisus sagitta* (F.) feeding on greater wax moth larvae, *Galleria mellonella* (L.).

The lipid content in the insect fat body plays a crucial role in the process of allocating energy reserves because lipids provide long-term storage of metabolic energy (Downer 1985). High lipid content in the fat body indicates conservation of energy, whereas the reverse suggests investment in such processes as reproduction or dispersal (Brough and Dixon 1989, Mason et al. 1989). In *P. maculiventris*, more lipid was found in the fat body of females that were provided less food than those provided abundant prey (Legaspi and O'Neil 1994). In evaluating life history trade-offs in *P. maculiventris*, (J.C.L., unpublished data) suggested that the predator stored lipids under conditions of food scarcity as a survival tactic. Only after metabolic needs are met is energy invested in reproduction.

The spined soldier bug is a generalist predator found throughout North America (Torre-Bueno 1939) in a variety of cropping systems. *P. maculiventris* feeds on >75 species of insect prey, primarily immature Coleoptera and Lepidoptera (McPherson 1980). Because of its relative prominence in crops, the biology of *P. maculiventris* has been extensively studied (for example, Mukerji and Le Roux 1965; Warren and Wallis 1971; Drummond et al. 1984; Legaspi and O'Neil 1993, 1994; O'Neil and Wiedenmann 1990; Wiedenmann and O'Neil 1991). However, few studies have been field-based (but see Evans 1982, O'Neil 1988, Wiedenmann and O'Neil 1992), or have addressed the physiologic state of predators in the field. In this article, we report the amount of stored fat in field-collected *P. maculiventris*, as well as their body

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[1] Current address: Texas Agricultural Experiment Station, 2415 East Highway 83, Weslaco, TX 78596.

[2] Department of Entomology, Purdue University, West Lafayette, IN 47907.

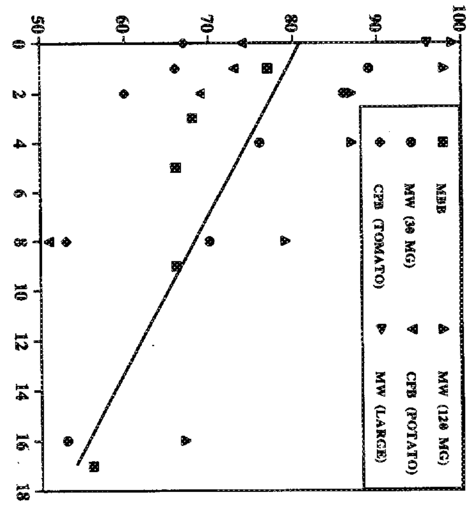

Fig. 1. Laboratory measurements of body weights of *P. maculiventris* under different feeding intervals. Females were provided 1 prey item at different feeding intervals with ad libitum treated as 0-d intervals. Data are pooled for different prey types MBB, Mexican bean beetle (Legaspi 1991); MW, small (30 mg) and large (120 mg) mealworms, respectively (O'Neil and Wiedenmann 1990); CPB, 15-mg Colorado potato beetle (Valicente 1991); MW (large) (Valicente 1991). The regression of body weight against feeding interval is $y = 80.85 - 1.58x$ (line drawn) which was used as the basis for comparison of field-collected predators (see text for details).

weights during the summers of 1988 and 1989. We compare fat reserves, egg loads on dissection, and body weights of female *P. maculiventris* collected from the field with those that were provided prey under various feeding regimens in the laboratory. Our objectives were to describe the physiologic condition of predators in the field and estimate from field collections their relative feeding frequency in the field.

Materials and Methods

Field Sampling. *P. maculiventris* were collected at 24-h intervals (excluding most weekends) using either sweep nets or pheromone traps in 8 field sites in Indiana from April to October in 1987 to 1989. Seven fields were located near Lafayette, IN, and consisted of the following sites and crops planted: airport (alfalfa), Bryan (potato), West Lafayette (fallow), Newman (alfalfa), Scholer (alfalfa), Throckmorton Farm (soybeans), and the veterinary farm (alfalfa). An additional site in Bedford, Lawrence County (alfalfa), was sampled approximately weekly. Pheromone trap sampling was done in the airport site (in 1987), West Lafayette (1988), and Newman site (1987–1989). Traps were made of covered clear plastic containers (19 cm in diameter) with 3 cone-shaped wire meshed openings on the sides around each trap. A glass vial filled

Table 1. Mean body weights ± SE of collected *P. maculiventris* regardless of sampling technique

Site	1987		1988		1989		Total	
	Male	Female	Male	Female	Male	Female	Male	Female
Airport (alfalfa)	39.8 ± 0.88 (126)	52.2 ± 1.25 (166)	—	—	—	—	39.8 ± 0.88 (126)	52.2 ± 1.25 (166)
Bedford (alfalfa)	54.8 ± 10.9 (5)	74.1 ± 2.9 (51)	0 ± 0 (0)	46 ± 0 (1)	—	—	54.8 ± 10.9 (5)	73.6 ± 2.9 (52)
Bryan (potato)	—	—	—	—	53.9 ± 1.8 (8)	86.2 ± 4.1 (4)	53.9 ± 1.8 (8)	86.2 ± 4.1 (4)
W. Lafayette (fallow)	—	—	34.3 ± 2.3 (18)	51.8 ± 3.5 (15)	0 ± 0 (0)	37 ± 0 (1)	34.3 ± 2.3 (18)	50.9 ± 3.4 (16)
Newman (alfalfa)	42.8 ± 1.4 (16)	59.5 ± 1.6 (35)	41.9 ± 2.2 (23)	54.9 ± 2.9 (40)	43.1 ± 0.8 (118)	57.9 ± 1.2 (188)	42.9 ± 0.7 (157)	57.7 ± 1.0 (263)
Scholer (alfalfa)	—	—	53.7 ± 5.6 (3)	84.7 ± 0.9 (3)	43 ± 0 (1)	78.5 ± 20.5 (2)	51 ± 4.8 (4)	82.2 ± 6.7 (5)
Throckmorton (soybeans)	39.7 ± 4.2 (4)	76.6 ± 2.2 (83)	41 ± 0 (1)	0 ± 0 (0)	46.5 ± 2.5 (2)	0 ± 0 (0)	41.9 ± 2.6 (7)	76.6 ± 2.2 (83)
Veterinary farm (alfalfa)	53.8 ± 1.7 (20)	84.7 ± 2.4 (52)	—	—	—	—	53.8 ± 1.7 (20)	84.7 ± 2.4 (52)
Total	42.2 ± 0.8 (171)	65.4 ± 1.1 (387)	39.6 ± 1.7 (45)	55.5 ± 2.3 (59)	43.9 ± 0.8 (129)	58.6 ± 1.2 (195)	42.5 ± 0.6 (345)	62.4 ± 0.8 (641)

Body weights are categorized according to sampling site, sex, and year the insects were collected. The crop planted to each site is indicated in parentheses. The numbers in parentheses below indicate size of sample. Totals summed across time are shown in the rightmost columns, total summed across sites in the bottom row. —, Field was not sampled.

Table 2. Mean body weights ± SE of *P. maculiventris* collected using pheromone traps

Site	1987		1988		1989		Total	
	Male	Female	Male	Female	Male	Female	Male	Female
Airport	39.2 ± 0.9 (118)	50.1 ± 1.2 (151)	—	—	—	—	39.2 ± 0.9 (118)	50.1 ± 1.2 (151)
W. Lafayette	—	—	34.3 ± 2.3 (18)	51.8 ± 3.5 (15)	—	—	34.3 ± 2.3 (18)	51.8 ± 3.5 (15)
Newman	42.1 ± 1.4 (14)	60.2 ± 1.5 (31)	41.9 ± 2.2 (23)	51.9 ± 2.5 (37)	43.1 ± 0.8 (116)	57.9 ± 1.2 (186)	42.8 ± 0.7 (153)	57.3 ± 1.0 (254)
Total	39.5 ± 0.8 (132)	51.8 ± 1.0 (182)	38.5 ± 1.7 (41)	51.9 ± 2.0 (52)	43.1 ± 0.8 (116)	57.9 ± 1.2 (186)	40.8 ± 0.6 (289)	54.5 ± 0.8 (420)

See Table 1 footnotes for interpretation of table.

with pheromone mixture (Aldrich 1988) and a cotton wick was taped vertically inside the trap. The active ingredient of the trap is based on the male sex pheromone and is attractive to females. The pheromone mixture was replaced at least once a week or whenever the vial needed to be refilled. Four traps at about a 15-m distance were hung on trees around the fields. Sweep net sampling was performed on all 8 sites according to the following schedule: airport (1987), Bedford (1987, 1988), Bryan (1989), West Lafayette (1989), Newman (1987 to 1989), Scholer (1988, 1989), Throckmorton (1987–1989), and the veterinary farm (1987). Fields were sampled by performing 20 sweeps with a 15-cm diameter sweep net along a diagonal transect of the field. In addition, predators were collected occasionally by hand and added to the sweep net collections.

Podisus maculiventris collected in the field were brought back to the laboratory and live body weights were measured using a Mettler AE100 Balance (±0.1 mg precision) (Mettler Instrument, Princeton, NJ). A subset of *P. maculiventris* from the Newman field was selected for lipid and egg load analyses. These females were caught using the pheromone method during the summers of 1988 and 1989 and were sacrificed and dissected after recording the body weights. The common field and collection method was intended to reduce experimental variability in comparisons between the 2 yr. To measure the dry weights of the egg masses, the ovaries were removed, oven dried at 40–50°C, placed in a plastic container, and weighed using the Mettler balance. Individual weights per egg were estimated by dividing the egg mass weight by the number of eggs per mass. Egg loads were also measured both in terms of numbers of mature eggs and the weights of egg masses.

To measure lipid content of fat body, the dorsal and ventral abdominal body walls to which most of the fat body is attached were separated and dried in an oven (40–50°C) for 3 d (see Legaspi and O'Neil 1994). The dry weight of the body walls was taken. The walls were then kept in individual glass vials and stored in a freezer (-10°C) for further lipid analysis. The fat body attached to the body walls was analyzed for lipid content (relative to the dry weight of body walls of *P. maculiventris*) using techniques described originally by Bligh and Dyer (1959) and modified by Legaspi (1991). To account

Table 3. Mean body weights ± SE of *P. maculiventris* collected using sweep nets

Site	1987		1988		1989		Total	
	Male	Female	Male	Female	Male	Female	Male	Female
Airport	49.6 ± 4.2 (8)	73.8 ± 5.1 (15)	—	—	—	—	49.6 ± 4.2 (8)	73.8 ± 5.1 (15)
Bedford	54.8 ± 10.9 (5)	74.1 ± 2.9 (51)	0 ± 0 (0)	46 ± 0 (1)	—	—	54.8 ± 10.9 (5)	73.6 ± 2.9 (52)
Bryan	—	—	—	—	53.9 ± 1.8 (8)	86.2 ± 4.1 (4)	53.9 ± 1.8 (8)	86.2 ± 4.1 (4)
W. Lafayette	—	—	—	—	0 ± 0 (0)	37 ± 0 (1)	0 ± 0 (0)	37 ± 0 (1)
Newman	47.5 ± 4.5 (2)	57.5 ± 8.4 (4)	0 ± 0 (0)	91.7 ± 4.1 (3)	43.5 ± 7.5 (2)	59.0 ± 18.0 (2)	45.5 ± 3.8 (4)	67.8 ± 7.8 (9)
Scholer	—	—	53.7 ± 5.6 (3)	84.7 ± 0.9 (3)	43 ± 0 (1)	78.5 ± 20.5 (2)	51 ± 4.8 (4)	82.2 ± 6.7 (5)
Throckmorton	39.7 ± 4.2 (4)	76.6 ± 2.2 (83)	41 ± 0 (1)	0 ± 0 (0)	46.5 ± 2.5 (2)	0 ± 0 (0)	41.9 ± 2.6 (7)	76.6 ± 2.2 (83)
Veterinary farm	53.8 ± 1.7 (20)	84.7 ± 2.4 (52)	—	—	—	—	53.8 ± 1.7 (20)	84.7 ± 2.4 (52)
Total	51.3 ± 1.9 (39)	77.4 ± 1.4 (205)	50.5 ± 5.0 (4)	82.1 ± 6.4 (7)	50.3 ± 1.9 (13)	73 ± 7.6 (9)	51.0 ± 1.4 (56)	77.3 ± 1.3 (221)

See Table 1 footnotes for interpretation of table.

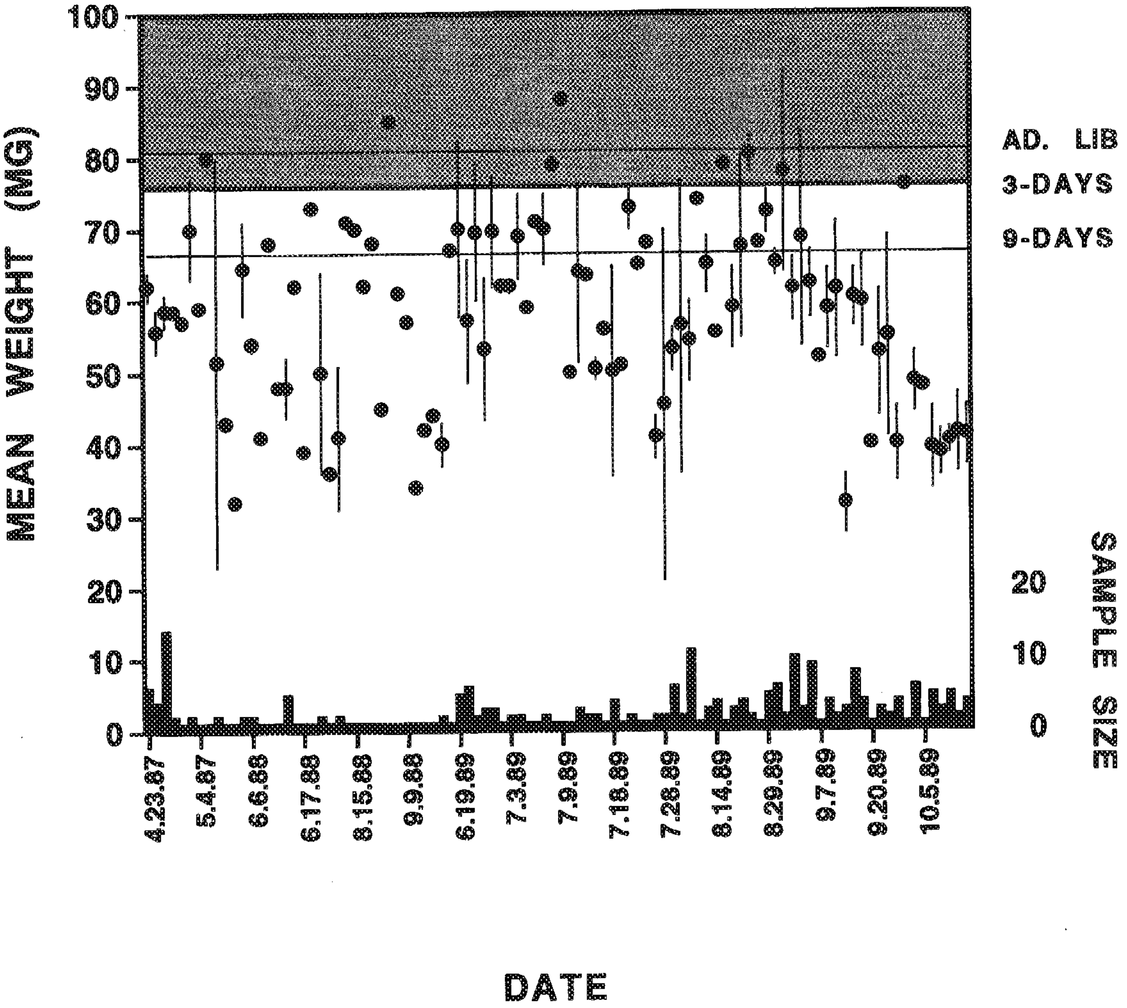

Fig. 2. Mean body weights ± SE of female *P. maculiventris* collected by pheromone traps in the Newman site, Indiana, from April 1987 to October 1989. The histogram at the bottom indicates the number of predators collected on each date. The solid lines indicate the mean body weights of females provided prey ad libitum or 1 prey item every 3 or 9 d in the laboratory. The shaded area denotes feeding rates corresponding to ad libitum and every 3 d.

for differences in body size of females, the dry weight of lipids per female (milligrams) was divided by the dry weight of the body wall (milligrams).

All statistical analyses were performed using the Systat Statistical Package (Wilkinson et al. 1992). Body weights were analyzed using 2-way analysis of variance, lipid contents, and egg numbers were analyzed using *t*-tests. Means were separated using the Tukey test and all error limits were set at $\alpha = 0.05$. Laboratory data on body weights as affected by feeding interval were analyzed by linear regression.

Previous Laboratory Findings

Body Weight. The body weight of *P. maculiventris* has been measured in the laboratory a number of times. O'Neil and Wiedenmann (1990) fed predators 2 sizes (≈30 and 120 mg) of *T. molitor* L. at 6 feeding intervals. In a similar study, Legaspi and O'Neil (1993) used Mexican bean beetle, *Epilachna varivestis* (Mulsant), larvae (≈35 mg) as prey, feeding predators under 5 feeding intervals. Valicente (1991) fed predators Colorado potato beetle, *Leptinotarsa decemlineata* (Say), larvae (≈15 mg), which were raised on either potato, *Solanum tuberosum*, or tomato, *Lycopersicon esculentum*, plants. Predators were fed under 4 feeding intervals, and an additional treatment of predators fed ad libitum (120 mg mealworms) was also included. In both of these studies, unmated female predators were used, predator body weight was measured frequently (every 1–3 d), and feeding regimes included treatments where predators were fed a single prey over increasingly longer time intervals (for example, 1 prey every 1, 2, 4, 8, and

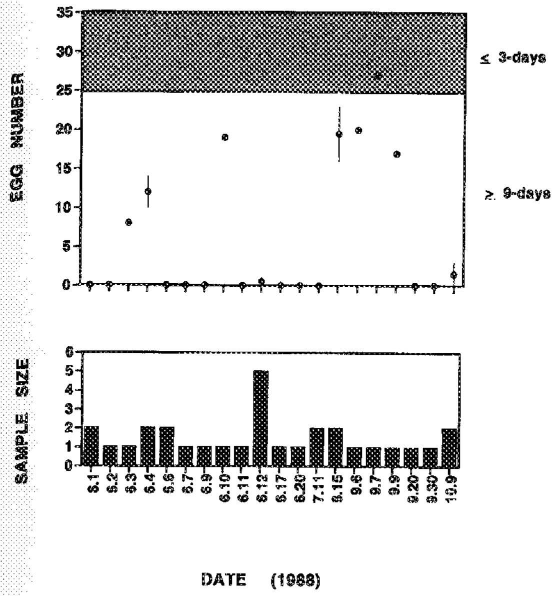

Fig. 3. Mean number of stored eggs ± SE of *P. maculiventris* females collected with pheromone traps from the Newman site, Indiana, from June to October 1988. The histogram beneath the graph indicates the number of individuals collected on each date. The shaded area indicates egg numbers ≥25, corresponding to laboratory predators fed 1 prey item at intervals of 3 d or less (see text).

16 d). No comparable information is available for male or mated *P. maculiventris*. The daily fluctuations in body weights of predators followed a similar pattern that reflected the feeding interval. Typically, predators fed well (for example, ad libitum or 1 prey daily) increased their weight to a plateau that was maintained throughout most of their lives (O'Neil and Wiedenmann 1990, Valicente 1991, Legaspi and O'Neil 1993). At longer feeding intervals (more than or equal to every 2 d), predator body weight fluctuated with a periodicity that reflected the feeding interval (in the work cited). Average lifetime body weights were influenced by the type of prey and the feeding interval, but in general, average body weight declined as the feeding interval increased (Fig. 1). A highly significant model ($Y = 80.85 - 1.58x$), although 1 with a relatively low r^2 ($F = 12.36$; $P < 0.002$; df = 1, 23; $r^2 = 0.35$) was found by regression analysis of body weight (milligrams) to feeding interval (days) (where ad libitum was equated to zero days between meals),

An estimate of body weight can be determined by solving the regression equation with specific number of days between a feeding. Thus, predators fed ad libitum (0 days between meals), or 1 prey every 1, 3, and 9 d, are expected to weigh 80.9, 79.3, 76.1, and 66.6 mg, respectively. These values will be used to compare the body weights of females collected in the field with those of females with a given feeding frequency in the laboratory.

Lipids and Stored Eggs. Legaspi and O'Neil (1994) report the effects of diet on *P. maculiventris* reproduction and lipid reserves. Treatments included predators fed 35 mg Mexican bean beetle larval prey at the following frequencies, ad libitum, and 1 prey every 3 and 9 d. They found that as the feeding interval increased, predators laid fewer eggs, had more stored lipids, and tended to have fewer eggs stored in their ovaries. Statistical analysis of the data suggested only dietary effects on lipids and stored eggs, and no statistically significant effects of age or age × diet interactions (Legaspi 1991, table 8, p. 98). Like studies of body weight (in the work cited), data are for unmated females. There are no estimates of lipid content of males or mated females.

The effect of age and feeding interval on lipids and stored eggs of *P. maculiventris* in the laboratory is presented in Legaspi and O'Neil (1994, table 1, p. 1256). For comparison with field data, we used the range of values for average lipid content and the number of stored eggs. Thus, field-collected predators with as much as 0.275 mg lipid per milligram of abdominal wall weight (dry weight), correspond to laboratory-reared females fed ad libitum to 1 prey every 3 d. Predators with ≥0.275 mg/mg correspond to females fed a single prey at intervals greater than every 3 d. For stored eggs, predators with ≥25 eggs correspond to females fed ad libitum to 1 prey every 3 d. Predators with <25 eggs correspond to females fed a single prey at intervals greater than every 3 d.

Results

In total, 986 *P. maculiventris* were caught (Table 1). Females were sampled more frequently than males, with 641 females and 345 males collected. Females weighed more than males ($F = 293.9$; df = 1, 984; $P < 0.01$). On average, females weighed 62.4 mg (SE = 0.8, $n = 641$) and males weighed 42.5 mg (SE = 0.6, $n = 345$). Both male and female weight differed among field sites (males: $F = 11.2$; df = 7, 337; $P < 0.01$; females: $F = 38.6$; df = 7, 633; $P < 0.01$) and between years (males: $F = 3.1$; df = 2, 342; $P < 0.05$; females: $F = 11.5$; df = 2, 638; $P < 0.01$).

Average body weights of predators caught using the pheromone traps and sweep nets are shown in Tables 2 and 3, respectively. Comparisons using t-tests of the body weights of predators caught in the same field and year indicated no consistent difference in samples of predator weights using the 2 sampling methods. At the airport site in 1987, predators caught with sweep nets were heavier than those sampled by pheromone traps (males: $t = 2.4$, df = 124, $P < 0.05$, females: $t = 4.5$, df = 164, $P < 0.01$). However, no weight differences caused by sampling method were found at the Newman site for 1987 and 1989 (1987: males, $t =$

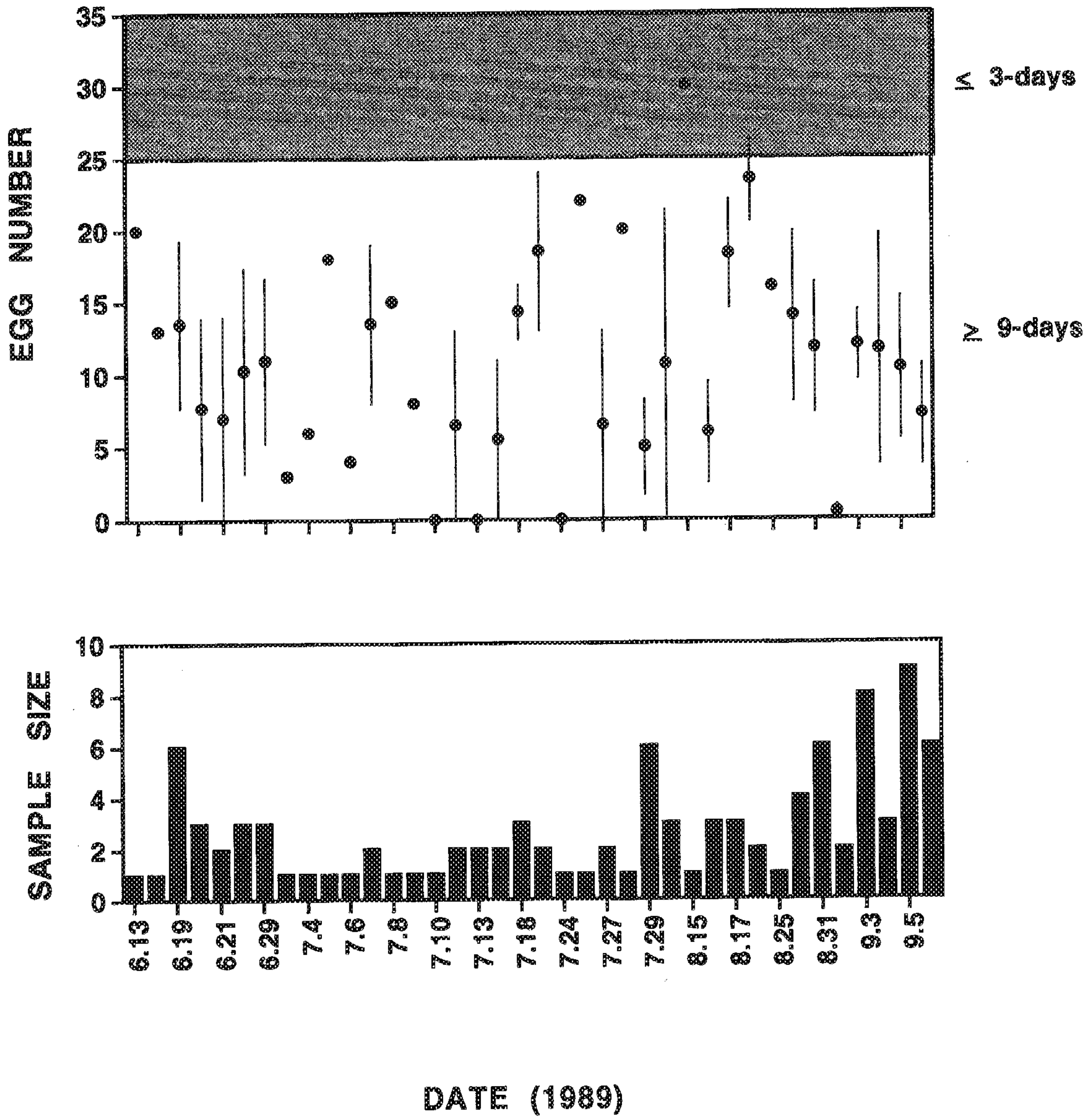

Fig. 4. Mean numbers of stored eggs ± SE dissections of *P. maculiventris* females collected with pheromone traps from the Newman site, Indiana, from June to September 1989 (graph format as in Fig. 3).

1.1, df = 14, $P > 0.05$, females, $t = 0.3$, df = 33, $P > 0.05$) (1989: males, $t = 0.05$, df = 116, $P > 0.05$, females, $t = 0.06$, df = 186, $P > 0.05$) (1988 data not analyzed because of small samples sizes collected).

Approximately 66.4% (257/387) of females in 1987, 84.8% (50/59) in 1988, and 86.7% (169/195) in 1989 weighed <76.1 mg, the laboratory-estimated body weight of a female fed every 3 d. As an example, Fig. 2 shows the changes in body weights of females collected in the field using pheromone traps from April 1987 to October 1989. The mean laboratory estimates of body weight as a function of feeding interval are superimposed on the field data as indicated by the lines. The shaded area corresponds to feeding rates of ad libitum to once every 3 d.

The number of stored eggs of females collected with pheromone traps at Newman field in 1988 and 1989 are shown in Figs. 3 and 4 (shaded area suggests higher predation rates). Both the average number of eggs and their weights were significantly higher in 1989 (average number = 11.0, SE = 1.0, $n = 102$; average weight = 3.1 mg, SE = 0.28, $n = 93$) versus 1988 (average number = 5.3, SE = 1.5, $n = 30$; average weight = 1.5 mg, SE

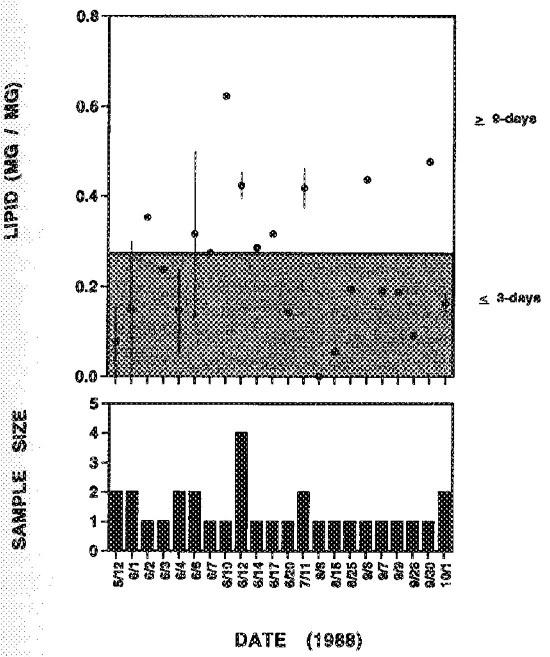

Fig. 5. Mean ± SE lipid content in mg/mg body wall of *P. maculiventris* females collected with pheromone traps from the Newman site, Indiana, from May to October 1988. The shaded area indicates lipid contents ≤0.275 mg/mg, which corresponds to laboratory females fed 1 prey item at intervals of 3 d or less (see text).

= 0.46, n = 28) ($t_{\text{number}} = 3.1$; $P < 0.01$; $t_{\text{weight}} = 2.99$; $P < 0.01$). No significant difference was found for average weight per egg in 1988 (average = 0.27 mg, SE = 0.01, n = 9) versus 1989 (average = 0.31, SE = 0.02, n = 66) (t = 1.8; $P > 0.05$). In 1988, 63.3% (19/30) of the females collected had no eggs at dissection (Fig. 3). In contrast, 26.5% (27/102) of females had no eggs at dissection in 1989. In 1988, 33% (10/30) predators had stored egg counts ranging from 1 to 25, corresponding to predators fed 1 prey item at intervals of 3 d or greater in the laboratory. Only 1 predator had >25 stored eggs, corresponding to predators fed every 3 d to ad libitum in the laboratory. In contrast, field-collected predators in 1989 had generally higher numbers of stored eggs. The corresponding percentages are 61.8% (63/102) containing 1–25 stored eggs and 11.8% (12/102) for >25 eggs, respectively.

The lipid content of females collected with pheromone traps at Newman field in 1988 and 1989 are shown in Figs. 5 and 6 (shaded area suggests higher predation rates). The average amount of lipid was higher in 1988 (average = 0.262 mg/mg body wall, SE = 0.02, n = 31) versus 1989 (average = 0.135 mg/mg, SE = 0.013, n = 147) (t = 3.9; $P < 0.01$). In 1988, 48.4% (16/31) had lipid levels ≥0.275 mg/mg, corresponding to laboratory females fed a single prey at intervals greater than every 3 d. Three females (9.7%) had no detectable lipid. In contrast, only 15.6% (23/147) females had lipid contents ≥0.275 mg/mg in 1989 and 30.6% (45/147) had no detectable lipids.

Discussion

The data on body weights (Tables 1–3), numbers of eggs at dissection (Figs. 3 and 4), lipid content (Figs. 5 and 6) and the average weight of eggs suggest that females in the field are prey-limited and consume somewhere on the order of single prey, roughly the size of a 3rd-instar Mexican bean beetle (35 mg), every 3 d. This conclusion is consistent with previous measures of attack rates of *P. maculiventris* in soybeans and potatoes. In soybeans, O'Neil (1988) and Wiedenmann and O'Neil (1992) found that females attack an average of 0.5 prey (4th and 3rd instar Mexican bean beetle, respectively) per day or 1 prey every 2 d. R.J.O. (unpublished data) measured its attack rate in potatoes against 3rd-instar Colorado potato beetle, and again found that the predator attacks an average of 1 prey every 2 d. Only when predators are given prey in numbers that reflect unrealistic field densities of prey do predators show attack rates >1 prey per day (see O'Neil 1989).

Estimates of predator body and egg weights also support the conclusion that predators are prey limited in the field. For example, Aldrich (1986) reported that overwintered females weighed an average of 47.4 mg (n = 95). Morris (1963) reported an average body weight of 54 mg for females reared from field-collected nymphs. Evans (1982) showed that the body size of field-collected females were less than females reared in the laboratory, a finding he attributed to lower encounter prey rates for predators in the field compared with those reared in a laboratory situation. Finally, the average weight of eggs in 1988 and 1989 was not significantly different and ranged between 27 to 31 mg. Previous estimates of egg weight by O'Neil and Wiedenmann (1990), Legaspi and O'Neil (1994) and Valicente (1991) have shown egg weights ranging from 34 to 48 mg, for predators fed as little as a single prey every 17 d.

Females collected in 1988 had higher lipid content and smaller egg loads than females collected in 1989 (Figs. 3–6). Legaspi and O'Neil (1994) have shown that as prey input levels decline, predators store more lipids and produce fewer eggs. These findings of yearly differences in lipid content and egg load, suggest predators consumed relatively fewer prey in 1988 than 1989. One possible explanation for these yearly differences is that in 1988, Indiana suffered a significant drought (Changnon 1991). Field sampling (unpublished data) reports to the Indiana Cooperative Extension Service (Gibb and Bledsoe 1988), and collections of *P. maculiventris* (Table 1) suggest that many insect population densities were lower in 1988 than 1989. That predator body weight was not signifi-

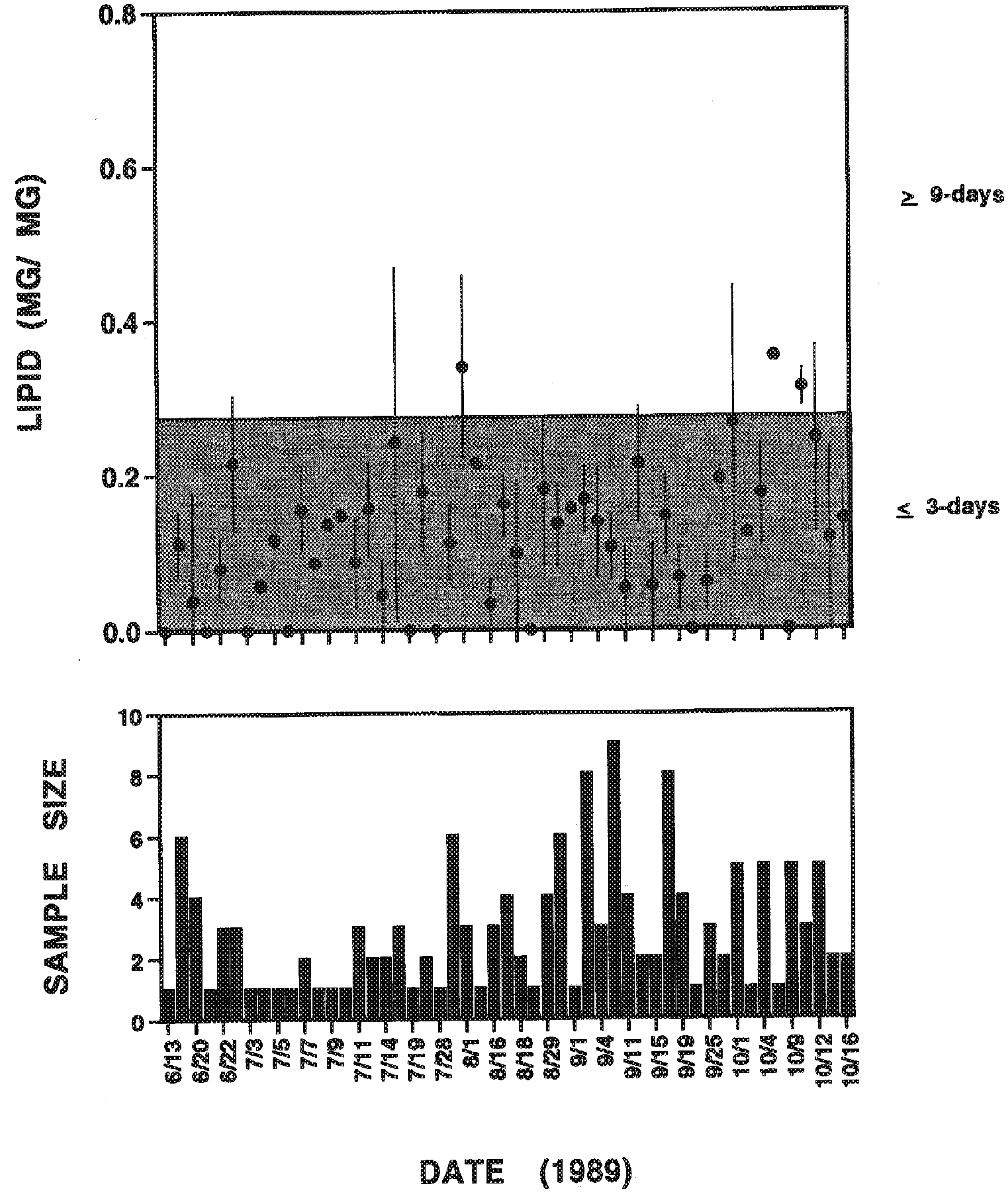

Fig. 6. Mean ± SE lipid content in mg/mg body wall of *P. maculiventris* females collected with pheromone traps from the Newman site, Indiana, from June to October 1989 (graph format as in Fig. 5).

cantly different between years (Tables 1–3) suggests that if there were drought-related differences in prey availability, predators responded by channeling the biomass from prey they did capture into maintenance rather than reproduction. Although not conclusive, the effect of a drought on potential prey populations is suggested by the physiologic state of predators in the field. More conclusive findings await more detailed study of weather-related effects on both prey and predator dynamics and predator physiology.

Our conclusions of the relative physiologic state and underlying rates of predation, must be tempered with caution. First and foremost we are extrapolating laboratory findings to the field. The relative constancy of the laboratory environment and low search requirements to obtain food, stand in contrast to the field environment. Even though we have attempted to mimic realistic field densities of prey in our laboratory studies of *P. maculiventris*, we can not duplicate the vagrancies of the field. Further, generalist predators like *P. maculiventris* can have a diversified menu of prey and plant-derived nutrients in their diet that affect their body weight, longevity, and reproductive output (Legaspi 1991, Valicente 1992). Variations in predator/prey dynamics may have influenced our samples and age-related physiology obscured trends. Finally, our use of pheromone traps to capture females for subsequent dissection may have given a biased sample of actual field populations because the pheromone acted as a sex attractant.

However, even with these caveats we are left with the general impression that female *P. maculiventris* experience low rates of predation. Although we have previously suggested this from field-cage measures of attack rates in 2 crops (O'Neil 1988, Wiedenmann and O'Neil 1992, R.J.O. unpublished data), this is the 1st indication from uncaged individuals. The implications of predators limited by how many prey they consume are varied and we have discussed several in related articles (for example, O'Neil 1988, Wiedenmann and O'Neil 1991, Wiedenmann and O'Neil 1992). If we have a biased estimate of predator attacks rates, we compound this error in further conclusions of, for example, predator ability to prevent pest outbreaks or the consequences of specific foraging strategies. We suggest that other predators may also be limited by the number of prey they encounter and that estimates of predation under conditions that mimic field densities will reveal low attack rates and concurrent life history adaptations to low prey inputs. When we have a broader base of study of predation under low prey inputs, we will be able to draw more definitive conclusions from field collections of predators.

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References Cited

Aldrich, J. R. 1986. Seasonal variation of black pigment under the wings in a true bug (Hemiptera: Pentatomidae): a laboratory and field study. Proc. Entomol. Soc. Wash. 88: 409–412.

1988. Chemistry and biological activity of pentatomid sex pheromones, pp. 417–431. *In* H. G. Cutler [ed.], Biologically active natural products: potential use in agriculture. American Chemical Society, Washington, DC.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–917.

Brough, C. N., and A.F.G. Dixon. 1989. Intra-clonal trade-off between reproductive investment and size of fat body in the vetch aphid, *Megoura viciae* Buckton. Funct. Ecol. 3: 747–751.

Changnon, Jr., S. 1991. Agricultural impacts and adjustments to the drought of 1988–1989. Research Report 91-01 Midwestern Climate Center, Champaign, IL.

Chua, T. H., and E. Mikil. 1989. Effects of prey number and stage on the biology of *Cyrthorinus lividipennis* (Hemiptera: miridae): a predator of *Nilaparvata lugens* (Homoptera: Delphacidae). Environ. Entomol. 18: 251–255.

De Clerq, P., and D. Degheele. 1992. Influence of feeding interval on reproduction and longevity of *Podisus sagitta* (Het.: Pentatomidae). Entomophaga. 37: 583–590.

Downer, R.G.H. 1985. Lipid metabolism, pp. 77–114. *In* G. A. Kerkut and L. I. Gilbert [eds.], Comprehensive insect physiology, biochemistry and pharmacology, vol. 8. Pergamon, Frankfurt.

Drummond, F. A., R. L. James, R. A. Casagrande, and H. Faubert. 1984. Development and survival of *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), a predator of the Colorado potato beetle (Coleoptera: Chrysomelidae). Environ. Entomol. 13: 1283–1286.

Evans, E. W. 1982. Consequences of body size for fecundity in the predatory stinkbug, *Podisus maculiventris* (Hemiptera: Pentatomidae). Ann. Entomol. Soc. Am. 75: 418–420.

Gibb, T. J., and L. W. Bledsoe. 1988. Population and behavior modifications of selected arthropod pests in Indiana during the 1988 drought. Proc. Indiana Acad. Sci. 98: 201–206.

Legaspi, J. C. 1991. Life history and fat reserves of the predator *Podisus maculiventris* (Heteroptera: Pentatomidae) under low inputs of the prey *Epilachna varivestis* (Coleoptera; Coccinellidae). Ph.D. dissertation, Purdue University, West Lafayette, IN.

Legaspi, J. C., and R. J. O'Neil. 1993. Life history of *Podisus maculiventris* given low prey numbers of *Epilachna varivestis* as prey. Environ. Entomol. 22: 1192–1200.

1994. Lipids and egg production of *Podisus maculiventris* (Heteroptera: Pentatomidae) under low rates of predation. Environ. Entomol. 23: 1254–1259.

McPherson, J. E. 1980. A list of the prey species of *Podisus maculiventris* (Hemiptera: Pentatomidae). Gt. Lakes Entomol. 13: 18–24.

Mason, L. J., S. J. Johnson, and J. P. Woodring. 1989. Influence of carbohydrate deprivation and tethered flight on stored lipid, fecundity, and survivorship of the soybean looper (Lepidoptera: Noctuidae). Environ. Entomol. 18: 1090–1094.

Morris, R. F. 1963. The effect of predator age and prey defense on the functional response of *Podisus* *maculiventris* Say to the density of *Hyphantria cunea* Drury. Can. Entomol. 95: 1009–1020.

Mukerji, M. K., and E. J. Le Roux. 1965. Laboratory rearing of a Quebec strain of the pentatomid predator, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). Phytoprotection. 46: 40–60.

O'Neil, R. J. 1988. Predation by *Podisus maculiventris* (Say) on Mexican Bean Beetle (*Epilachna varivestis* Mulsant), in Indiana soybeans. Can. Entomol. 120: 161–166.

1989. Comparison of laboratory and field measurements of the functional response of *Podisus maculiventris* (Heteroptera: Pentatomidae). J. Kans. Entomol. Soc. 62: 148–155.

1990. Functional response of arthropod predators and its role in the biological control of insect pests in agricultural systems, pp. 83–96. *In* P. E. Dunn [ed.], New directions in biological control: alternatives for suppressing agricultural pests and diseases. Wiley, New York.

O'Neil, R. J., and R. N. Wiedenmann. 1990. Body weight of *Podisus maculiventris* (Say) under various feeding regimens. Can. Entomol. 122: 285–294.

Santos, M. A. 1982. Effects of low prey densities on the predation and oviposition of *Zetzellia mali* (Acarina: Stigmaeidae). Environ. Entomol. 11: 972–974.

Torre-Bueno, J. R. de la 1939. A synopsis of the Hemiptera-Heteroptera of America north of Mexico. Part I. Entomol. Am. 19: 141–310.

Valicente, F. 1991. Effects of two host plants on selected life history characteristics of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). M.S. thesis, Purdue University, West Lafayette, IN.

Warren, L. O., and G. Wallis. 1971. Biology of the spined soldier bug *Podisus maculiventris* (Hemiptera: Pentatomidae). J. Ga. Entomol. Soc. 6: 109–115.

Wiedenmann, R. N., and R. J. O'Neil. 1990. Effects of low rates of predation on selected life-history characteristics of *Podisus maculiventris* (Heteroptera: Pentatomidae) Can. Entomol. 122: 271–283.

1991. Searching behavior and time budgets of the predator *Podisus maculiventris*. Entomol. Exp. Appl. 60: 83–93.

1992. Searching strategy of the predator *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). Environ. Entomol. 21: 1–9.

Wilkinson, L., Hill, M., and E. Vang. 1992. SYSTAT: statistics, version 5.2 ed. Systat, Evanston, IL.

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